

# A NEW RHINOCEROS FROM THE LOWER MIOCENE OF THE BUGTI HILLS, BALUCHISTAN, PAKISTAN: THE EARLIEST ELASMOTHERIINE

by PIERRE-OLIVIER ANTOINE *and* JEAN-LOUP WELCOMME

**ABSTRACT.** The stratigraphical position of the Dera Bugti area (Baluchistan, Pakistan), which yielded the remains described herein, is discussed. Dental and postcranial material attributed to *Bugtirhinus praecursor* gen. et sp. nov., from the lower Miocene (MN 3) of the same area, is described. This species is the oldest and most primitive member of the elasmotheriine group within Rhinocerotidae (Mammalia). A new diagnosis is established for the Elasmotheriini. Comparison with the other lower and middle Miocene elasmotheriine taxa leads to the tree [*Bugtirhinus praecursor* [*Caementodon oettingenae* [other elasmotheriine taxa]]]. An upper Oligocene–lowermost Miocene Asiatic differentiation is suggested for the group, strengthened by a first appearance datum in the Dera Bugti area (lower part of the MN 3). The origin and dispersal of the elasmotheriines throughout Eurasia are discussed and correlated with major faunal exchanges.

**KEY WORDS:** Bugti Hills, Pakistan, Rhinocerotidae, Elasmotheriini, Miocene, biostratigraphy, palaeobiogeography.

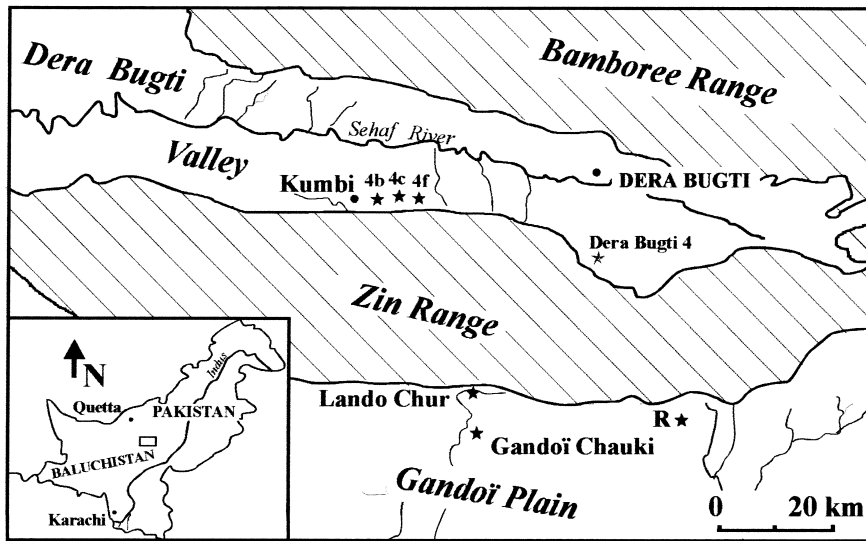
**TERTIARY** continental layers from the Bugti Hills (Baluchistan, Pakistan) have yielded many fossil mammals. In these faunas, rhinocerotoids are very abundant and diversified. The rhinoceroses have essentially been collected and studied since the beginning of the twentieth century (Lydekker 1881, 1884; Pilgrim 1910, 1912; Forster-Cooper 1924, 1934). Since then, only the French palaeontological expeditions in the Bugti Hills area (Text-fig. 1), managed by one of us (JLW) and Prof. L. Ginsburg during 1995–1999 have collected new rhino material (Welcomme *et al.* 1997; Welcomme and Ginsburg 1997; Welcomme *et al.* 1999).

Forster-Cooper (1934) attributed several specimens to *Ceratorhinus tagicus* [i.e. *Protaceratherium minutum* (Cuvier, 1822)]. Then, Heissig (1972, 1974, 1976) recognized in some of them a primitive elasmotheriine, named *Caementodon* sp. The elasmotheriines form a group considered to be closely related to the extant rhinoceroses. The material consisted of two maxillary fragments discovered near Dera Bugti, in lower Miocene layers.

Since then, the French expeditions in this area have collected thousands of vertebrate specimens, with macro- and micromammals, reptiles and fishes (Welcomme *et al.* 1997; Welcomme and Ginsburg 1997). Thirty dental and postcranial remains from a minute and primitive elasmotheriine have been discovered in a few sites near Dera Bugti. Their morphology is comparable to Heissig's *Caementodon* sp. and leads us to establish a new taxon.

## STRATIGRAPHICAL SETTING

The stratigraphical position of the 'Bugti fauna' has always been a problem. Pilgrim (1908) described a geological section of the Dera Bugti area: a 'Stampian' marine sand, covered by continental deposits with several 'Aquitanian' fossiliferous levels. The main taxa present (e.g. mastodonts, rhinos and suids) typically characterize the Miocene, but some of them (e.g. *Anthracotherium*, *Paraceratherium*, *Cadurcotherium*) resemble Oligocene forms. Moreover, Jacobs *et al.* (1981) mentioned a rodent fauna, discovered 'near' Dera Bugti, and very similar to the Eocene Chappatimyidae. Later, these rodents were considered by Flynn *et al.* (1986) to be a new endemic Miocene group, the Baluchimyinae. Are they endemic



TEXT-FIG. 1. Map of the Bugti Hills (Baluchistan, Pakistan) showing the localities referred to in this work. Sites with *Bugtirhinus praecursor* gen. et sp. nov. in bold face (after Welcomme and Ginsburg 1997).

survivors or are the faunas mixed, as Pickford (1988) wondered? To solve the problem, the total geological section was studied again by Welcomme *et al.* (1997). Then, Welcomme and Ginsburg (1997) proved that the 'Bugti fauna' was a set of distinct faunas in distinct areas. In fact, Eocene-like rodents and Oligocene-like large mammals mainly come from Palaeogene deposits in the Gandoi Plain area to the south of the Zin anticline ('Zen Koh Range' in Welcomme and Ginsburg, 1997). By contrast, the Dera Bugti area corresponds to the northern side of it (Text-fig. 1).

The latter area essentially contains Miocene deposits (Welcomme and Ginsburg 1997). Successive fossiliferous levels were labelled 0–6 sup. and first attributed to the lower Miocene by Welcomme *et al.* (1997). Since then, the results of the last expedition in March–April 1999 (Welcomme *et al.* 1999) definitely proved that levels 0–3 correspond to Palaeogene deposits (with *Paraceratherium*, *Cadurcotherium*, *Anthracotherium* and entelodonts). Level 3' did not yield any proboscidean nor *Paraceratherium* remains. Levels 4–6 sup. (with mastodonts, deinotheres and no more *Paraceratherium*) are definitely later than the Eurasia-Africa collision responsible for the Proboscidean Datum Event (Madden and Van Couvering 1976). Levels 5 and 6 are respectively correlated with the Mein's (1975, 1979, 1990) mammal zones MN 3b and the basal MN 4 owing to the presence of rodents (*Prokanisamys*).

The only level that has yielded the primitive elasmotheriine (Text-fig. 2) is the fossiliferous continental level 4 (localities Kumbi 4b–c, f and Dera Bugti 4), corresponding to the classical site of Kumbi (Pilgrim 1908, 1912). The associated fauna comprises six species of rhinoceroses (Welcomme *et al.* 1997). Some (*Aprotodon fatehjangense*, '*Dicerorhinus*' *shahbazi* and *Plesiaceratherium* sp.) are respectively closely comparable to *Brachypotherium heinzlini*, *Dicerorhinus leakeyi* and *Aceratherium acutirostratum*, recognized in Napak and Songhor by Hooijer (1966). The radiometric age of Songhor is 19.6 Ma (Pickford 1986) and Napak is older (Tassy 1986). *D. cf. parvum* is present all along the section. Its type area is Rusinga, for which Schmidt-Kittler (1987) has given a radiometric age of around 17.8 Ma. Nevertheless, *Dorcatherium* is present at Meswa Bridge, the earliest Miocene site in Africa, around 22 Ma (Pickford 1986). Level 4 has also yielded *Bunolistriodon affinis* (Pilgrim, 1908); in the opinion of Made (1996), this primitive bunodont suid (named *Listriodon pentapotamiae* by Welcomme *et al.* 1997) is only known in Kumbi (type locality) and Songhor. Level 4 is also the lowest one in the area with recognizable proboscideans: a primitive *Gomphotherium* sp. and *Prodeinotherium pentapotamiae*. The oldest sites with comparable proboscideans in Africa are Legetet, around 20 Ma, and Songhor (Tassy 1986).

| Ma         | EPOCH            | AGE           | STAGE       | Mammal Zone | AFRICA | CENTRAL/EASTERN ASIA        |                         | WESTERN ASIA       | EUROPE                |         |                   |                 |
|------------|------------------|---------------|-------------|-------------|--------|-----------------------------|-------------------------|--------------------|-----------------------|---------|-------------------|-----------------|
|            |                  |               |             |             |        | Pakistan                    | China, Mongolia         |                    | Iberia                | France  |                   |                 |
| 15         | Mid MIOCENE      | SERRAVALLIAN  | ASTARACIAN  | MN 7-8      |        | Chinji Formation            | <u>Tung Gur</u>         | <u>Sofca</u>       |                       |         |                   |                 |
|            |                  |               |             | MN 6        |        |                             | <u>Kadirpur</u>         | <u>Erlanggang</u>  | <u>Yeni Eskihisar</u> | Simorre |                   |                 |
|            |                  | LANGHIAN      |             |             |        |                             | <u>Kanatti Chak</u>     | <u>Lengshuigou</u> | <u>Pasalar</u>        | Sansan  |                   |                 |
|            | <u>Mochiwala</u> |               |             |             |        | <u>Tongxin</u>              | <u>Belometchetskaja</u> | Lisbon             | <u>Faluns</u>         |         |                   |                 |
|            | 20               | Early MIOCENE | BURDIGALIAN | ORLEANIAN   | MN 4   | Rusinga                     | L. Bugti Fm             | Bugti 6-6 sup.     |                       |         | <u>Córcoles</u>   | <u>Montréal</u> |
|            |                  |               |             |             | MN 3   | Songhor<br>Legetet<br>Napak |                         | <b>Bugti 4</b>     |                       |         | <u>Pellecahus</u> |                 |
| AQUITANIAN |                  | AGENIAN       |             |             |        |                             | Bugti 3'                |                    |                       |         |                   |                 |
|            |                  |               |             |             |        |                             | MN 1                    | Meswa              |                       |         |                   |                 |

TEXT-FIG. 2. Stratigraphical position of the Dera Bugti Formation. Biostratigraphical correlations with Old World Provinces for early and middle Miocene. Layers with *Bugtirhinus praecursor* gen. et sp. nov. are in bold face. Sites that have yielded elasmotheriines are underlined (after Heissig 1972; Pickford 1986; Tassy 1986; Ginsburg *et al.* 1987; Qiu 1990; Bruijn *et al.* 1992; Made 1996, 1997; Rögl 1996; Antoine 1997; Iñigo and Cerdeño 1997; Welcomme and Ginsburg 1997; Welcomme *et al.* 1997).

The Bugti faunas show a strong African character, and a good correlation can be made between Songhor and level 4 (Text-fig. 2). An equivalent age of around 19.6 Ma can be stated for it, corresponding to the lower MN 3 in Europe. Made (1997) was of the same opinion, on the basis of ancient collections, and correlated the entire 'Bugti fauna', together with Songhor, with the MN 3 zone.

#### METHODS

The dental terminology is that proposed by Heissig (1969, pp. 11–12; 1972, pp. 9–10). Measurements (in mm) were taken by POA, except when mentioned.

Isolated postcranials were attributed to this new taxon owing to their strong resemblance with those from other primitive elasmotheriines: *Caementodon oettingenae* Heissig, 1972, *Hispanotherium matritense* (Lartet, in Prado, 1864) and *Aegycitherium beonensis* Antoine, 1997. Moreover, their small size (even for adult remains) distinguishes them from other associated rhinoceroses.

*Abbreviations.* TD, transverse diameter; APD, antero-posterior diameter; H, height; L, length; W, width (when different from TD); D, distance (between two elements); r, right; l, left; prox., proximal; dist., distal; med., medial; mid., middle; lat., lateral; ant., anterior; post., posterior; sup., superior; max., maximum; min., minimum; juv., juvenile; fgt, fragment; trochl., trochlea; fac., facet; art., articulation; tuber., tuberosity; ext., extremity; Calc., calcaneum; Pyram., pyramidal; Rad., radius; S.-L., semilunate; Trap., trapezium; Trapzd., trapezoid; orig., original.

Order PERISSODACTYLA Owen, 1858  
Superfamily RHINOCEROTOIDEA Owen, 1845  
Family RHINOCEROTIDAE Owen, 1845  
Subfamily RHINOCEROTINAE Owen, 1845  
Tribe ELASMOTHERIINI Bonaparte, 1845

*Type genus.* *Elasmotherium* Fischer, 1808.

*Other genera.* *Sinotherium* Ringström, 1923; *Iranotherium* Ringström, 1924; *Procoelodonta* Matthew, 1931, *Hispanotherium* Crusafont and Villalta, 1947; *Begertherium* Beliajeva, 1971; *Caementodon* Heissig, 1972; *Beliajevina* Heissig, 1974; *Ninxiatherium* Chen, 1977; *Tesselodon* Yan, 1979; *Aegycitherium* Antoine, 1997.

Genus *BUGTIRHINUS* gen. nov.

*Type species.* *Bugtirhinus praecursor* sp. nov.

*Derivation of name.* From *Bugti*, the name of the tribe living in the Dera Bugti area, and the Greek *rhis*, rhinos, meaning nose (as in *rhinoceroses*).

*Diagnosis.* That of the type species, the only one attributed to the genus (see below).

*Bugtirhinus praecursor* sp. nov.

Plate 1, figures 1–11; Plate 2, figures 1–12; Text-figure 3

- |       |  |
|-------|--|
| p1934 | 'referred to <i>Ceratorhinus tagicus</i> '; Forster-Cooper, p. 601, pl. 65, figs 26, 28. |
| 1974  | <i>Caementodon</i> sp.; Heissig, p. 25.  |
| 1976  | <i>Caementodon</i> sp.; Heissig, p. 19.  |
| 1997  | <i>Caementodon oettingenae</i> ; Welcomme <i>et al.</i> , p. 532.                        |
| 1997  | <i>Coementodon oettingenae</i> ; Welcomme and Ginsburg, p. 1001, tab.                    |

*Derivation of specific name.* From the Latin *praecursor*, precursor. This new species is both the oldest and most primitive elasmotheriine described so far. It represents the sister group of all other elasmotheriines.

*Holotype.* M 15361, right M1-/M3/series from the Dera Bugti area (Pakistan), stored in The Natural History Museum, London. M3/ is a germ.

*Type horizon and locality.* *B. praecursor* gen. et sp. nov. is known from several sites in the lower Miocene (lower part of the MN 3) of the Bugti Hills (Baluchistan, Pakistan).

*Paratype.* M 15363, left series with D1/, D2/ and D3/ from the Dera Bugti area (Pakistan), stored in The Natural History Museum, London.

*Referred material.* Kumbi 4c (corresponding to classical 'Gaj of Kumbi'): Pak 80, right M3/. Kumbi 4b: Pak 742, left I1/ (worn); Pak 750, left P2/; Pak 753, left P4/; Pak 752, right P4/; Pak 762, right M3/; Pak 736, left I/2 (female); Pak 747, left P/3; Pak 791, right Mc IV (distal fragment); Pak 788, right astragalus; Pak 792, left Mt II (distal fragment). Kumbi 4f: Pak 1655, right M2/ (without ectoloph); Pak 1674, left M/2 (fragment); Pak 1702, right radius (distal fragment); Pak 1711, left scaphoid; Pak 1712, right scaphoid; Pak 1708, left unciform; Pak 1707, right unciform; Pak 1681, left astragalus (fragment); Pak 1718, left navicular; Pak 1992, left ectocuneiform; Pak 1738, left Mt III (proximal fragment); Pak 1741, right Mt IV (proximal fragment); Pak 1746, right second phalanx Mt II. Dera Bugti 4: Pak 1984,

TABLE 1. *Bugtirhinus praecursor* gen. et sp. nov., Dera Bugti Formation, Baluchistan, Pakistan. Anterior dentition: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997).

| Taxa                        | I1/            |                 |             | I2        |                |           |             |                 |
|-----------------------------|----------------|-----------------|-------------|-----------|----------------|-----------|-------------|-----------------|
|                             |                | L               | APD         | W         |                | H         | W           | total L         |
| <i>A. beonensis</i>         | N              | 2               | 2           | 4         | N              | 9         | 10          | 7               |
|                             | Range          | 101-107         | 35-36       | 14-20     | Range          | 16-24     | 19-30       | 97-112          |
|                             | Mean           | 104             | 35.5        | 17        | Mean           | 19        | 24.1        | 104             |
| <i>C. oettingenae</i>       | N=1            | -               | 22          | 9         | N=2            | 11-12     | 30          | -               |
| <i>H. matritense</i> *      | N              | -               | -           | -         | N              | 6         | 6           | -               |
|                             | Range          | -               | -           | -         | Range          | 13-19.5   | 19.6-30.3   | -               |
|                             | Mean           | -               | -           | -         | Mean           | 15.53     | 25.07       | -               |
| <b><i>B. praecursor</i></b> | <b>Pak 742</b> | <b>(&gt;35)</b> | <b>(22)</b> | <b>10</b> | <b>Pak 736</b> | <b>15</b> | <b>(23)</b> | <b>(&gt;70)</b> |

right magnum (posterior fragment); Pak 1989, left calcaneum (*Tuber calcanei*); Pak 2001, right Mt III (distal fragment); Pak 2003, right Mt III (distal fragment). These specimens are stored in the Muséum National d'Histoire Naturelle, Paris.

**Diagnosis.** Slender rhinocerotid with semi-circular I1/ in cross-section, cement filling up the cheek teeth, partially fused roots on upper cheek teeth, strong lingual wall on P2-4/, transverse metaloph on P2/, short metaloph on M1/ and especially M2, trefoil-shaped protoloph on M3/, without labial cingulum on lower cheek teeth, with strong mesostyle on upper deciduous teeth, posterior contact between scaphoid and semilunate, oblique fibular facet on astragalus, high and narrow *Tuber calcanei*, rectangular navicular in vertical view, sigmoid upper border on MtIII, continuous pad-shaped posterior tuberosity on MtIV.

### Description

Neither cranial nor mandibular remains have been found.

**Anterior dentition.** Two incisors are preserved. The left I1/ (Pak 742) is worn, partly broken and enamel has disappeared (Pl. 1, fig. 3). Nevertheless, we can attribute it to a primitive elasmotheriine, because of its small size, feeble antero-posterior development (Table 1) and the semicircular cross-section of the root (rounded in the external side).

The left I2 (Pak 736) is also worn, without enamel, but the root is almost complete (Pl. 1, fig. 4). The posterior part of the grinding surface is preserved, flat transversally, slightly concave sagittally, with a semicircular posterior outline. The tooth is small (Table 1), but normally developed. Its morphology (small size, normal development, pear-like cross-section) leads us to attribute this specimen to a primitive elasmotheriine. It was probably a female, owing to the smooth curvature of the root and the presence of two sagittal depressions (respectively stronger and absent in males).

**Upper dentition.** The upper cheek teeth are small (Tables 2–3), with undulated ectoloph. The premolar series is very short in comparison with the molar series. Cement is abundant (Pl. 1, figs 8, 10b) on the molars (filling up the valleys, cingula and folds), and less on the premolars (only present on one P4/). The premolars and the M2/ (Pak 1655) are worn and low-crowned, whereas the nearly unworn M2/ (M 15361) and M3/ crowns are higher, but still brachyodont. The crowns are very conical (not prismatic). The enamel is rather thin, especially in the valleys, finely vertically striated on most of the crown, shagreened on its top.

**Premolars.** P2/ (Pak 750) is small and worn. The ectoloph is undulating (Pl. 1, fig. 5a), with very strong paracone and metacone ribs. The parastyle is short and straight. The prefossette is triangular and narrow. The protoloph is directed backwards, thickening lingually, with a strong protocone and no constriction. The metaloph is transverse, continuous, without crochet. The protocone and hypocone are joined, equally developed, forming a lingual wall. Nevertheless, a shallow groove separates both lingual cusps on the whole height of the crown (Pl. 1, fig. 5b). A small fold on the lingual

TABLE 2. *Bugtirhinus praecursor*, upper premolars: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997); \*\* after Yan (1979).

| Taxa                       |         | P2/         |         |           |       | P4/     |         |         |             |       |
|----------------------------|---------|-------------|---------|-----------|-------|---------|---------|---------|-------------|-------|
|                            |         | L           | ant W   | post W    | H     | L       | ant W   | post W  | H           |       |
| <i>A. beonensis</i>        | N       | 2           | 2       | 2         | 2     | N       | 2       | 1       | 2           | 1     |
|                            | Range   | 24-29       | 30-31   | 34-37     | 8-26  | Range   | 32-40   | 46      | 44-45       | 42    |
|                            | Mean    | 26.5        | 30.5    | 35.5      | 17    | Mean    | 36      | 46      | 44.5        | 42    |
| <i>Beg. grimmi</i>         | N       | 2           | 2       | 2         | 2     | N       | 3       | 3       | 2           | 2     |
|                            | Range   | 30-30.5     | 31-34.5 | 33-38     | 18-41 | Range   | 30-38.5 | 50-51.5 | 42-48       | 28-34 |
|                            | Mean    | 30.25       | 32.75   | 35.5      | 29.5  | Mean    | 34.17   | 50.67   | 45          | 31    |
| <i>Beg. tekkayai</i>       | N=1     | 29          | 29      | 31        | -     | N=1     | 33      | 46      | 51          | 58    |
| <i>Bef. caucasica</i>      | N=1     | 29          | 29      | 34.5      | 27    | N=1     | -       | 36      | -           | -     |
| <i>C. oettingenae</i>      | N=1     | 26          | 26      | 28.5      | 25    | N=1     | -       | -       | -           | -     |
| <i>H. matritense</i> *     | N       | 10          | -       | 10        | -     | N       | 10      | -       | 11          | -     |
|                            | Range   | (19.1)-25.7 | -       | 25.8-32.9 | -     | Range   | 29.5-37 | -       | (39.5)-48.3 | -     |
|                            | Mean    | 24.76       | -       | 29.87     | -     | Mean    | 31.83   | -       | 43.38       | -     |
| <i>B. praecursor</i>       | Pak 750 | 19.5        | 24      | 24.5      | 13.5  | Pak 753 | 25      | 36      | 32          | 19    |
|                            | -       | -           | -       | -         | -     | Pak 752 | (>25)   | (>32)   | 30          | 22    |
| <i>T. fangxianensis</i> ** | N=1     | 22          | 26.5    | 26        | -     | N=1     | 30      | 36.5    | 35          | -     |

side of the ectoloph corresponds to the paracone. There is no trace of secondary folds, in this stage of wear. The postfossette is also triangular, narrow and superficial.

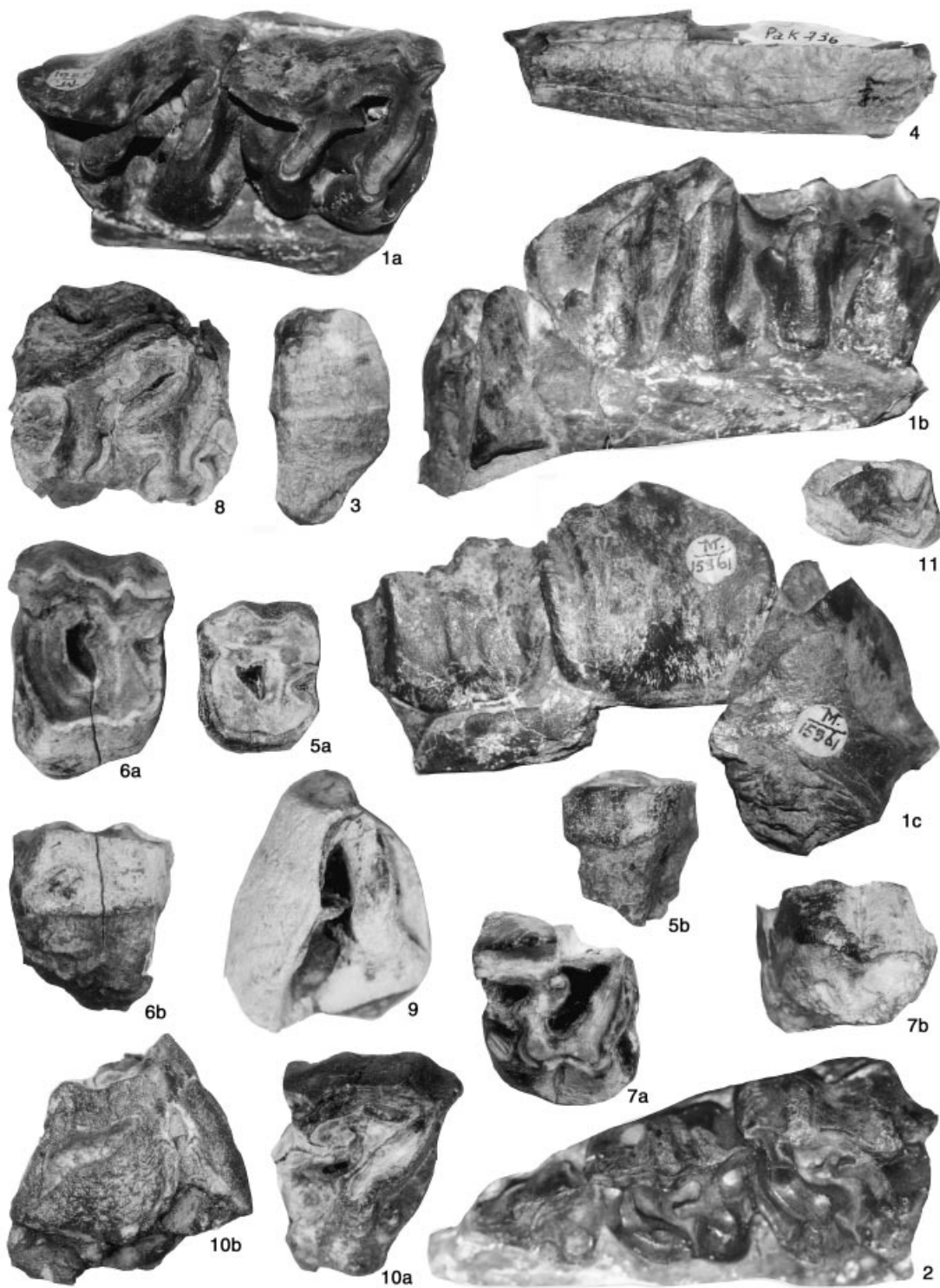
Anterior and posterior cingula are low and discontinuous because of wearing due to the contact with P1/ and P3/. Lingual cingulum is totally absent. Labial cingulum is limited to smooth and low oblique edges on parastyle and metastyle.

Two P4/ are preserved. The less weathered one (Pak 752) lacks the anterior part of the ectoloph (Pl. 1, fig. 7a). The metaloph is shorter than the protoloph. Paracone and metacone ribs are marked (stronger on Pak 753). Parastyle is straight and short, whereas the metastyle is very long. The protoloph is continuous, thickening lingually (Pak 752) and slightly curved backwards in its lingual half. A shallow anterolingual groove stretches the protocone, more markedly on Pak 752 (nearly absent on Pak 753). There is no trace of antecrochet. Protoloph and metaloph are strongly joined lingually, consequently closing the median valley (Pl. 1, figs 6b, 7b). A lingual groove separates them, vanishing in the lowermost millimetres of the crown. On Pak 753, another slight vertical groove deforms the hypocone posterolingually (Pl. 1, fig. 6a). The metaloph is continuous, straight and directed backwards, without constriction. Crochet is present, simple on both specimens, straight on Pak 753, curved and slightly plicated on Pak 752. The postfossette is triangular, relatively shallow (more superficial than the median valley). Labial cingulum is limited to low and smooth oblique edges on parastyle and metastyle. There is no trace of lingual cingulum. Posterior cingulum is conserved on Pak 752, with a median depression and a strong lingual development.

*Molars.* The two first molars [M1-/M2/ M 15361 (holotype) and M2/ Pak 1655] are constructed upon the same scheme, M2/ only being longer labially and narrower posteriorly than M1/, with a more massive hypocone (Pl. 1, figs 1a-b). These teeth have conical crowns, with lophs and folds thickening downwards. The ectoloph is rather flat, but paracone and metacone ribs are smoothly marked, as well as the mesostyle (Pl. 1, fig. 1c); parastyle is straight, not so long. By contrast, the metastyle is very long and the ectoloph curves outwards in its posterior part (M 15361). The protoloph is

## EXPLANATION OF PLATE I

Figs 1–13. *Bugtirhinus praecursor* gen. et sp. nov., Lower Miocene, level 4, Dera Bugti Formation, Baluchistan, Pakistan. 1a–c, M 15361, right M1-3/series, holotype. a, without M3/, occlusal view; b, lingual view; c, labial view. 2, M 15363, right D1-3/ series, paratype, occlusal view. 3, Pak 742, left I1/, Kumbi 4b, left side view. 4, Pak 736, left I/2 (female), Kumbi 4b, upper view. 5a–b, Pak 750, left P2/, Kumbi 4b. a, occlusal view; b, lingual view. 6a–b, Pak 753, left P4/, Kumbi 4b. a, occlusal view; b, lingual view. 7a–b, Pak 752, right P4/, Kumbi 4b. a, occlusal view; b, lingual view. 8, Pak 1655, right M2/, Kumbi 4f, occlusal view. 9, Pak 762, right M3/, Kumbi 4b, occlusal view. 10a–b, Pak 80, right M3/, Kumbi 4c. a, mesial view; b, occlusal view. 11, Pak 747, left P/3, Kumbi 4b, occlusal view. All figures  $\times 1$ .



ANTOINE and WELCOMME, *Bugtirhinus*

TABLE 3. *Bugtirhinus praecursor*, upper molars: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997); \*\* after Yan (1979).

| Taxa                      | M1/     |           |         |         | M2/      |           |         |        | M3/     |         |           |           |       |
|---------------------------|---------|-----------|---------|---------|----------|-----------|---------|--------|---------|---------|-----------|-----------|-------|
|                           |         | L         | ant W   | post W  |          | L         | ant W   | post W |         | L       | ant W     | post W    | H     |
| <i>A. beonensis</i>       | N       | 2         | 2       | 2       | N        | 3         | 3       | 3      | N       | 5       | 3         | 5         | 6     |
|                           | Range   | 49-50     | 51-52   | 47-48   | Range    | 55-57     | 56-57   | 48-50  | Range   | 48-53   | 50-54     | 55-57     | 21-48 |
|                           | Mean    | 49.5      | 51.5    | 47.5    | Mean     | 56        | 56.33   | 48.67  | Mean    | 50      | 51.67     | 55.8      | 30.5  |
| <i>Beg. grimmi</i>        | N=1     | (35.5)    | -       | -       | N=2      | 49 -      | 53 -    | 45 -   | N=2     | 42-48   | 47.5-57   | 49-61     | - 54  |
| <i>Beg. tekkavai</i>      | N=1     | (48)      | -       | -       | -        | -         | -       | -      | -       | -       | -         | -         | -     |
| <i>Bel. caucasica</i>     | N=1     | 47        | 48      | 42      | N=1      | (>45)     | 50      | -      | -       | -       | -         | -         | -     |
| <i>C. oettingenae</i>     | N=2     | 41.5-49   | 42-49   | 40.5-42 | N=1      | 50        | 46.5    | 40     | N=1     | -       | -         | 47        | -     |
| <i>H. matritense*</i>     | N       | 13        | 14      | -       | N        | 16        | 17      | -      | N       | 11      | 11        | 5         | -     |
|                           | Range   | 33.9-51.8 | 45-54.4 | -       | Range    | 38.7-52.6 | 45.3-60 | -      | Range   | 42-52.3 | 39.4-52.3 | 49.1-52.1 | -     |
|                           | Mean    | 41.53     | 49.71   | -       | Mean     | 47.16     | 51.34   | -      | Mean    | 46.04   | 46.26     | 51.5      | -     |
| <i>B. praecursor</i>      | M 15361 | 32        | 32      | 27      | M 15361  | 36.5      | 32      | 28     | Pak 80  | 38      | 38        | 43        | (>32) |
|                           | -       | -         | -       | -       | Pak 1655 | (>35)     | -       | -      | Pak 762 | 34      | 39        | 43        | (>34) |
| <i>T. fangxianensis**</i> | -       | -         | -       | -       | N=1      | -         | 48      | 42     | -       | -       | -         | -         | -     |

continuous, with strong anterior constriction and antecrochet in late stages of wear, isolating the protocone and almost leading, on worn teeth (Pak 1655), to a medifossette (Pl. 1, fig. 8). The median valley is open lingually on M1/ and M2/. There is no trace of lingual cingulum, except for M1/ (M 15361), which has a small cingular tubercle in the bottom of the median valley. No lingual groove is present at the base of the protocone on M2/ (both specimens). The strong crochet is straight, getting closer to the metacone downwards. The metaloph is continuous and short, especially on M2/ where the crochet is the same length. Neither crista nor secondary folds are developed. The postfossette is deep and narrow. The anterior cingulum, high on M1/, occupies the whole anterior side. Labial cingulum is generally absent. There are still low tubercles on M1/ (M 15361). Owing to a horizontal cross-section on the holotype (contemporaneous to Forster-Cooper), relationships between the roots are known: on both M1/ and M2/, the labial roots are totally separated, whereas the lingual ones strongly join each other.

The M3/ are triangular. The parastyle is marked, forming an obtuse angle with the ectometaloph (Pl. 1, figs 9, 10a). The protoloph is continuous, sigmoid, with strong anterior constriction and antecrochet at the base of the crown ('trefoil-shaped'). The lingual side of the protocone is very long and flat, without any groove. The median valley is filled up with cement, wide open lingually, with a small enamel tubercle in its entrance. The ectometaloph is convex, without any constriction. A strong sagittal crochet almost joins the antecrochet. The former is simple on Pak 762 and probably M 15361 but clearly plicated on Pak 80.

*Upper deciduous teeth.* D1/-D3/ left series (M 15361). The crowns are conical, with convex ectolophs (Pl. 1, fig. 2). The lingual cusps are always separate (molariform milk teeth). There are probably traces of cement in the valleys of D2/ and D3/. There is no trace of labial cingula nor cristae on the complete series. D1/ is very small (Table 4), with a strong and straight parastyle. Paracone and metacone ribs are thick. The protoloph is discontinuous and low, with a reduced protocone. The metaloph is continuous, without crochet, but with a strong hypocone. Lingual cusps are distinct. The wide postfossette narrows on its bottom. Anterolingual cingulum is strong, vanishing on the protocone.

On D2/, the protoloph is strongly curved backward, wrapping the anterolingual part of the median valley. Protocone and hypocone almost join together. The prefossette is well developed. The strong parastyle is straight. The main rib on the ectoloph is the thick mesostyle, whereas paracone and metacone ribs are smooth. The continuous and transversal metaloph is deformed by a straight crochet, detached from the ectoloph. Some cingular traces lie on the lingual part of the protoloph.

D3/ lacks a mesostyle. By contrast, the metacone rib is strong. Even stronger is the paracone rib. The parastyle is reduced. The continuous protoloph is still curved backward, and stretched by both an anterior constriction and the strong antecrochet. On the wide metaloph, the crochet is strong, joined to the ectoloph, as in M1-2/. A shallow groove notches the anterolingual side of the hypocone. The postfossette is narrow. Lingual cingulum is reduced to a small tubercle on the hypocone. The posterior part of the metastyle is broken.

A cross-section, identical to that of the holotype, has been done. Morphology and relationships between the roots are the same: labial roots totally separated and lingual ones joined.

The left isolated D4/ from the Bugti Hills figured by Forster-Cooper (1934, pl. 65, fig. 30) certainly belongs to *B. praecursor*. Unfortunately, it has disappeared from the collection stored in the NHM.

*Lower dentition.* Only a left P/3 (Pak 747) and an anterior part of a left M1/-2 (Pak 1674) are preserved. The premolar is small and rectangular (Table 5; Pl. 1, fig. 11). Cement is covering the ectolophid as a thin layer. The crown is low



TABLE 4. *Bugtirhinus praecursor*, upper deciduous teeth: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997); \*\*\* after Fortelius (1990).

| Taxa                        |                | D1/       |           | D2/       |           |             | D3/             |             |           |
|-----------------------------|----------------|-----------|-----------|-----------|-----------|-------------|-----------------|-------------|-----------|
|                             |                | L         | post W    | L         | ant W     | post W      | L               | ant W       | post W    |
| <i>A. beonensis</i>         | N=1            | 23        | (22)      | 31        | 27        | 30          | 41 -            | 33 -        | 32 -      |
| <i>Beg. grimmi</i>          | -              | -         | -         | -         | -         | -           | -               | -           | -         |
| <i>Beg. tekkayai</i> ***    | N              | 1         | 3         | 2         | 3         | 3           | 4               | 4           | 5         |
|                             | Range          | 25        | 18.3-19.5 | 29-30     | 27.8-31.6 | 27.6-31.4   | 31.3-33         | 32.6-38.4   | 31-37     |
|                             | Mean           | 25        | 19.47     | 29.5      | 29.7      | 29.6        | 32.25           | 35.22       | 34.02     |
| <i>C. oettingenae</i>       | -              | -         | -         | -         | -         | 25          | 31              | 30          | 26        |
| <i>H. matritense</i> *      | N              | 13        | 12        | 5         | -         | 7           | 1               | -           | 3         |
|                             | Range          | 19-25.1   | 14.4-19.6 | 21.7-27.5 | -         | 13.3-26.8   | 33.4            | -           | 15.8-32.7 |
|                             | Mean           | 22.43     | 17.56     | 24.82     | -         | 22.09       | 33.4            | -           | 26.23     |
| <b><i>B. praecursor</i></b> | <b>M 15363</b> | <b>16</b> | <b>13</b> | <b>22</b> | <b>19</b> | <b>20.5</b> | <b>(&gt;22)</b> | <b>24.5</b> | <b>24</b> |

(about 10 mm), without any vertical rugosity. The trigonid is well developed, angular and forms a right dihedral. The paralophid is curved and retains the trace of contact with P/2. The external groove is deep but vanishes a few millimetres above the neck. Metaconid and entoconid are short of constrictions. The posterior valley is narrow sagittally, with a V-shaped bottom. The only traces of cingulum are restricted to the anterior part of the tooth: labially and lingually it forms a low, short and oblique edge, the latter being more developed.

The molar fragment consists in a incomplete trigonid, nearly unworn. The trigonid forms an angulous and right dihedral.

*Postcranial skeleton.* The only long bone preserved is a distal end of a right radius (Pak 1702). This piece belongs to an adult and is very small (Table 6; Pl. 2, fig. 1). It is a very slender bone. There is no trace of contact or fusion with the ulna on the lateral edge of the diaphysis, except distally there is a low semicircular articular surface. Closer to the distal end, a deep oblique groove, corresponding to the *M. extensorius carpi*, hollows the anterior face down to the scaphoid facet. In anterior view, the distal surface for the first carpal row on its whole width can be observed: this surface is raised forward. The distal side articulates with scaphoid, semilunar and pyramidal. The scaphoid facet is deep and high, with a quadrant outline and a high posterior triangular lip. The semi-lunar facet is trapezium-shaped (stretched backwards). The pyramidal facet is reduced to a small and narrow triangle (Text-fig. 3).

*Carpal bones.* These are small, high and slender. Both scaphoids are clearly higher posteriorly than anteriorly (Table 7). Tuberosities are lacking on the medial side. On the lateral side, there only are two facets for the semilunate, reaching the anterior border. Posterior to these real articular surfaces, a well-developed spur exists, corresponding to a contact zone with the semilunate. There are three facets on the distal side. The anterior one, for the magnum, is

TABLE 5. *Bugtirhinus praecursor*, lower dentition: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997).

| Taxa                        |                | P/3       |           |             |           | M/2             |           |             |          |                 |
|-----------------------------|----------------|-----------|-----------|-------------|-----------|-----------------|-----------|-------------|----------|-----------------|
|                             |                | L         | ant W     | post W      | H         | L               | ant W     | post W      | H        |                 |
| <i>A. beonensis</i>         | N              | 2         | 2         | 2           | 2         | N               | 5         | 4           | 6        | 5               |
|                             | Range          | 33        | 20        | 22          | 26-27     | Range           | 38-49     | 28-29       | 29-31    | 10-33           |
|                             | Mean           | 33        | 20        | 22          | 26.5      | Mean            | 45.8      | 28.25       | 29.83    | 22              |
| <i>Beg. grimmi</i>          | -              | -         | -         | -           | -         | N=2             | - 50      | - 29.5      | 24-30    | 21-30           |
| <i>Beg. tekkayai</i>        | N=2            | 31-33     | 18-20     | 18-21.5     | 21.5-45   | -               | -         | -           | -        | -               |
| <i>Bel. caucasica</i>       | N=1            | 29        | 17        | 18.5        | 23        | N=1             | 44.5      | 21.5        | 24       | (>32)           |
| <i>H. matritense</i> *      | N              | 22        | -         | 22          | -         | N               | 16        | -           | 17       | -               |
|                             | Range          | 22.3-31   | -         | 17.4-21.5   | -         | Range           | 39.3-44.6 | -           | 22-29.7  | -               |
|                             | Mean           | 27.04     | -         | 19.28       | -         | Mean            | 42.24     | -           | 26       | -               |
| <b><i>B. praecursor</i></b> | <b>Pak 736</b> | <b>23</b> | <b>14</b> | <b>14.5</b> | <b>12</b> | <b>Pak 1674</b> | <b>-</b>  | <b>(20)</b> | <b>-</b> | <b>(&gt;27)</b> |

TABLE 6. *Bugtirhinus praecursor*, radius: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997).

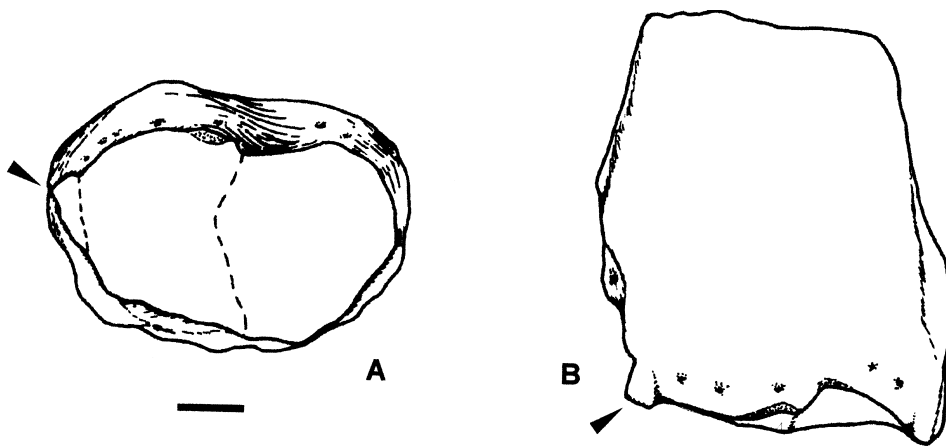
| Radius                 |          |            |           |            |           |
|------------------------|----------|------------|-----------|------------|-----------|
| Taxa                   |          | dist. ext. |           | dist. art. |           |
|                        |          | TD         | APD       | TD         | APD       |
| <i>A. beonensis</i>    | N        | 1          | 3         | 2          | 5         |
|                        | Range    | 87         | 60-64     | 71-72      | 38-43     |
|                        | Mean     | 87         | 61.67     | 71.5       | 39.6      |
| <i>Beg. grimmi</i>     | N=2      | 84-89      | 49(>50)   | 65-71      | 34-40     |
| <i>H. matritense</i> * | N        | 5          | 3         | 5          | 5         |
|                        | Range    | 70.4-77.2  | 49.3-57.2 | 60.4-68.9  | 33.9-38.7 |
|                        | Mean     | 73.88      | 53.27     | 65.24      | 36.7      |
| <i>B. praecursor</i>   | Pak 1702 | 50         | 38        | 47         | 27        |

triangular, transversally flat and concave sagittally (Pl. 2, fig. 2b). Backwards, the trapezoid facet is highly extending on the medial side (Pl. 2, fig. 2a). Finally, the trapezium facet is rounded and rather small.

A magnum (Pak 1984) is partly preserved, the whole anterior half lacking. The bone was high and narrow (Table 8), with a straight and rounded proximal apophysis, essentially corresponding to the semilunate. The posterior tuberosity is well developed, rather long and narrow, bent down (Pl. 2, fig. 3).

Two unciforms are also preserved. They are small and rather massive, with a well-developed posterior tuberosity (Table 9). The anterior face is pentagonal and not so high laterally, short of tuberosities, except a strong medial one, close to the junction of the semilunate and magnum facets (Pl. 2, fig. 4). In the postero-lateral corner of the pyramidal facet, a little vertical expansion, but the McV- and pyramidal facets are still not joined. On the distal side, the McV facet is very oblique transversally (at about 50 degrees with the horizontal). The posterior tuberosity is wide and flattened, rather long.

*Metacarpal bones.* The only one is a distal end of a right McIV. The bone is small and slender (Table 10), with proximally a rounded diaphysis cross-section. The diaphysis slightly enlarges distally. The trochlea, in distal view, is rectangular (narrow and deep), with a rounded anterior border. A big and acute postero-lateral expansion clearly exceeds the posterior border of the trochlea. The intermediate relief is evident in anterior view (Pl. 2, fig. 5), becoming higher and acute backwards.



TEXT-FIG. 3. *Bugtirhinus praecursor* gen. et sp. nov., Dera Bugti Formation, Baluchistan, Pakistan; Pak 1702, left radius (distal fragment). A, distal view; B, anterior view. Arrows mark the plesiomorphic pyramidal facet; scale bar represents 10 mm.

TABLE 7. *Bugtirhinus praecursor*, scaphoid: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997).

| Scaphoid              |          |           |           |        |        |         |                  |                     |      |                        |       |                       |       |
|-----------------------|----------|-----------|-----------|--------|--------|---------|------------------|---------------------|------|------------------------|-------|-----------------------|-------|
| Taxa                  |          | TD        | APD       | ant. H | mid. H | post. H | Rad.-fac.<br>APD | Trap.-fac.<br>H APD |      | Trapzd.-fac.<br>TD APD |       | Magnum-fac.<br>TD APD |       |
| <i>A. beonensis</i>   | N        | 2         | 2         | 3      | 3      | 3       | 3                | 3                   | 3    | 3                      | 3     | 2                     | 2     |
|                       | Range    | 44-46     | 57-64     | 44-51  | 38-45  | 60-65   | 42-43            | 15-16               | 6-8  | 27-31                  | 20-23 | 21-24                 | 26-29 |
|                       | Mean     | 45        | 60.5      | 47.67  | 42     | 62.67   | 42.67            | 15.67               | 7    | 28.67                  | 21.33 | 22.5                  | 27.5  |
| <i>Beg. grimmi</i>    | N=1      | 46        | 69        | 53     | 42     | 66      | 47               | 18                  | 11   | 31                     | 32    | (29)                  | 25    |
| <i>Bel. caucasica</i> | N=1      | 40        | 58        | 42     | -      | 55      | 40               | 16                  | 15   | -                      | -     | -                     | -     |
| <i>C. oettingenae</i> | N=2      | 39 -      | 56.5 -    | 35-40  | 30-36  | 43.5 -  | 32-37            | 11 -                | 13 - | 24 -                   | 19-20 | 20 -                  | 22 -  |
| <i>H. matritense*</i> | N        | 7         | 10        | -      | -      | 13      | 11               | -                   | -    | -                      | -     | -                     | -     |
|                       | Range    | 35.4-43.8 | 51.3-58.3 | -      | -      | 39.1-57 | 32.2-46.3        | -                   | -    | -                      | -     | -                     | -     |
|                       | Mean     | 40.79     | 56.4      | -      | -      | 51.08   | 39.18            | -                   | -    | -                      | -     | -                     | -     |
| <i>B. praecursor</i>  | Pak 1711 | 34        | 54        | 39.5   | 33     | 46.5    | 34               | 13                  | 9    | 21                     | 18    | 18.5                  | 20    |
|                       | Pak 1712 | (>36)     | (>53)     | (>40)  | 36     | 48      | 37               | 13                  | 8    | 24                     | 21    | 20                    | -     |

*Tarsal bones.* Two astragali are conserved. They are both small and high but massive in medial view and square-shaped in anterior view (Table 11). The trochlea is high, deep, asymmetrical, with a wider lateral lip. The lips are rounded. The medial border of the medial lip is vertical, nearly in contact with the medial tubercle on Pak 788. The contact between tibia- and fibular facet on the lateral lip forms quite a sharp edge. The fibular facet is oblique, not vertical at all, very slightly concave transversally, and really wide (Pl. 2, fig. 6a). It forms a salient strip in anterior view. *Collum tali* is very low and still lower medially, where it even vanishes on Pak 788. The medial tubercle is not very salient but clearly angular. The navicular facet proceeds onto the anterior face, so it is visible on its most part in anterior view. By contrast, the cuboid facet is only visible by its side-face, in the same view. The posterior side bears three articular facets for the calcaneum (Pl. 2, fig. 6b). The first (Cc1) is very deep in its upper part, triangle-shaped, with a wide and low latero-distal expansion. The second facet (Cc2) is oval, with a vertical axis and is perfectly flat. The third facet (Cc3), joined to the latter on its whole height, forms a horizontal strip. In distal view, trochlea and distal articulation almost share the same axis. In the posterior corner, a salient break ends the navicular facet, locking the navicular. The cuboid facet, on the lateral side of the articulation, forms a long and oblique flat strip, at about 45 degrees from the bone axis.

One *Tuber calcanei* (Pak 1989) has been attributed to *B. praecursor*. It is small, high and very narrow (Table 12; Pl. 2, fig. 7). Its section and posterior side form an isosceles triangle with a very acute top. In lateral view, the top of the *Tuber* is very salient.

TABLE 8. *Bugtirhinus praecursor*, magnum: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997).

| Magnum                |          |           |                      |       |
|-----------------------|----------|-----------|----------------------|-------|
| Taxa                  |          | H         | post. tuber.<br>TD H |       |
| <i>A. beonensis</i>   | N        | 3         | 2                    | 2     |
|                       | Range    | 51-55     | 31-32                | 22-26 |
|                       | Mean     | 52.67     | 31.5                 | 24    |
| <i>Beg. grimmi</i>    | N=1      | 54        | 22                   | 22    |
| <i>C. oettingenae</i> | N=1      | 41        | -                    | -     |
| <i>H. matritense*</i> | N        | 7         | -                    | -     |
|                       | Range    | 40.8-52.8 | -                    | -     |
|                       | Mean     | 46.73     | -                    | -     |
| <i>B. praecursor</i>  | Pak 1984 | (>36)     | (>15.5)              | 21    |

TABLE 9. *Bugtirhinus praecursor*, unciform: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997).

| Unciform               |          |           |           |           |           |              |       |             |       |             |       |           |       |
|------------------------|----------|-----------|-----------|-----------|-----------|--------------|-------|-------------|-------|-------------|-------|-----------|-------|
| Taxa                   |          | TD        | H         | max. APD  | APD       | post. tuber. |       | S.-L.-facet |       | Pyram.-fac. |       | McV-facet |       |
|                        |          |           |           |           |           | TD           | H     | TD          | APD   | TD          | DAP   | TD        | APD   |
| <i>A. beonensis</i>    | N        | 4         | 4         | 3         | 3         | 3            | 3     | 5           | 5     | 5           | 5     | 4         | 3     |
|                        | Range    | 57-65     | 51-62     | 74-85     | 64-71     | 34-38        | 20-24 | 29-34       | 25-31 | 38-43       | 28-32 | 22-23     | 28-31 |
|                        | Mean     | 59.25     | 54.25     | 79        | 66.67     | 35.33        | 22    | 31          | 28.8  | 40          | 30.4  | 22.75     | 29.67 |
| <i>Bel. caucasica</i>  | N=1      | 52        | 44        | 74        | 66        | 30           | 23    | (22)        | -     | (34)        | -     | -         | -     |
| <i>C. oettingenae</i>  | N=1      | 48.5      | 48        | -         | -         | -            | -     | 21.5        | 26.5  | (>23)       | 23    | -         | -     |
| <i>H. matritense</i> * | N        | 19        | 25        | 8         | 8         | -            | -     | -           | -     | -           | -     | -         | -     |
|                        | Range    | 39.7-59.1 | 32.3-45.9 | 52.5-78.9 | 41.2-60.4 | -            | -     | -           | -     | -           | -     | -         | -     |
|                        | Mean     | 49.77     | 39.18     | 67.8      | 52.51     | -            | -     | -           | -     | -           | -     | -         | -     |
| <i>B. praecursor</i>   | Pak 1708 | 42.5      | 38.5      | 59        | 48        | 23           | 14    | 23          | 22    | 24          | 23    | 16.5      | 23    |
|                        | Pak 1707 | 43.5      | 39        | -         | -         | -            | -     | 23          | 24.5  | 25          | 26    | 14        | -     |

TABLE 10. *Bugtirhinus praecursor*, McIV: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997).

| McIV                   |         |            |            |           |
|------------------------|---------|------------|------------|-----------|
| Taxa                   |         | dist. ext. | dist. art. |           |
|                        |         | max TD     | TD         | APD       |
| <i>A. beonensis</i>    | N       | 5          | 5          | 5         |
|                        | Range   | 42-47      | 35-40      | 32-37     |
|                        | Mean    | 43.8       | 37         | 34.2      |
| <i>Beg. grimmi</i>     | N=1     | 37         | 30         | 30        |
| <i>Bel. caucasica</i>  | N=1     | 38         | 33.5       | 30        |
| <i>H. matritense</i> * | N       | 11         | 11         | 10        |
|                        | Range   | 26.1-40    | 23.4-36.2  | 24.7-37.8 |
|                        | Mean    | 33.59      | 30.48      | 30.21     |
| <i>B. praecursor</i>   | Pak 791 | 21.5       | 20.5       | 24.5      |

A complete navicular (Pak 1718) is preserved. It is high, rectangular in proximal view (Table 13; Pl. 2, fig. 8). Proximally, the astragalus facet is rhomb-shaped. Its surface is convex transversally and regularly concave sagittally. The posterior part is bent up, with nevertheless a lateral hollow, corresponding to the connected astragalus relief. In lateral view, the two usual articular facets for the cuboid are fused. The fused cuboid facets and the astragalus facet are in contact on their whole length. The distal side bears three articular surfaces, very smoothly limited, responding to the

## EXPLANATION OF PLATE 2

Figs 1–12. *Bugtirhinus praecursor* gen. et sp. nov., Lower Miocene, level 4, Dera Bugti Formation, Baluchistan, Pakistan. 1, Pak 1702, left radius, Kumbi 4f, anterior view. 2a–b, Pak 1711, left scaphoid, Kumbi 4f. a, medial view; b, lateral view. 3, Pak 1984, right magnum (fragment), Dera Bugti 4, lateral view. 4, Pak 1707, right unciform, Kumbi 4f, anterior view. 5, Pak 791, right McIV (fragment), Kumbi 4b, anterior view. 6a–b, Pak 788, right astragalus, Kumbi 4b. a, anterior view; b, posterior view. 7, Pak 1989, left calcaneum (posterior fragment), Dera Bugti 4, posterior view. 8, Pak 1718, left navicular, Kumbi 4f, proximal view. 9, Pak 1992, left ectocuneiform, Dera Bugti 4, proximal view. 10a–b, Pak 1738, left MtIII (proximal fragment), Kumbi 4f. a, proximal view; b, anterior view. 11, Pak 2003, right Mt III (distal fragment), Dera Bugti 4, anterior view. 12, Pak 1741, right MtIV (proximal fragment), Kumbi 4f, anterior view. All figures  $\times 1$ .

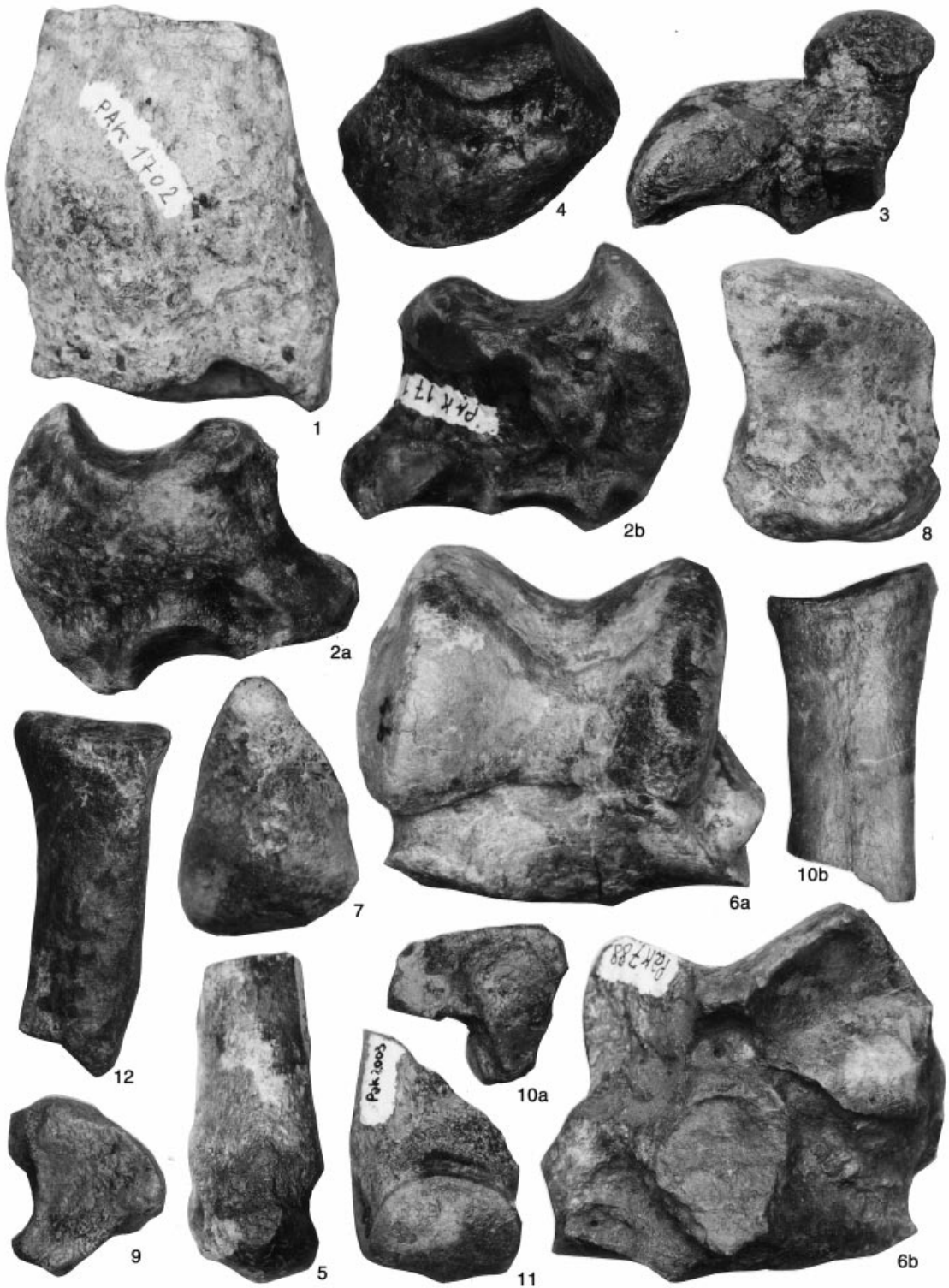


TABLE 11. *Bugtirhinus praecursor*, astragalus: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997).

| Astragalus            |          |         |           |         |           |       |       |             |       |             |       |             |           |             |       |
|-----------------------|----------|---------|-----------|---------|-----------|-------|-------|-------------|-------|-------------|-------|-------------|-----------|-------------|-------|
| Taxa                  |          | max TD  | trochl TD | max APD | H         |       |       | Calc.-fac.1 |       | Calc.-fac.2 |       | dlist. art. |           | Cuboid-fac. |       |
|                       |          |         |           |         | med.      | mid.  | lat.  | TD          | H     | TD          | H     | max TD      | APD       | L           | W     |
| <i>A. beonensis</i>   | N        | 9       | 9         | 7       | 9         | 9     | 6     | 7           | 6     | 7           | 6     | 9           | 8         | 7           | 9     |
|                       | Range    | 80-92   | 74-87     | 55-63   | 62-71     | 56-64 | 67-74 | 37-43       | 43-51 | 25-30       | 33-40 | 69-78       | 42-52     | 45-54       | 15-21 |
|                       | Mean     | 85-89   | 80-78     | 59-14   | 68        | 60-33 | 71    | 41-29       | 47    | 27-57       | 36-67 | 73-89       | 46-75     | 51-43       | 16-78 |
| <i>Beg. grimmi</i>    | N        | 7       | 8         | 8       | 6         | 6     | 6     | 67          | 7     | 7           | 7     | 7           | 7         | 6           | 7     |
|                       | Range    | 74-86   | 62-78     | 41-54   | 63-74     | 57-64 | 62-68 | 29-40       | 36-48 | 20-28       | 32-40 | 62-76       | 38-48     | 46-52       | 17-21 |
|                       | Mean     | 79-57   | 70-87     | 50-62   | 69-5      | 60-17 | 64-83 | 34-71       | 41-29 | 23-71       | 35-86 | 69-71       | 44-29     | 49-33       | 17-71 |
| <i>Bel. caucasica</i> | N=1      | 78      | 67        | 51      | 68        | 55    | 61    | (41)        | 42    | 18          | 37    | 69          | 42        | 46          | 18    |
| <i>C. oettingenae</i> | N        | 3       | 3         | 4       | 4         | 4     | 3     | 3           | 3     | 4           | 2     | 4           | 4         | 4           | 3     |
|                       | Range    | 58-59   | 47-53     | 37-41   | 45-52     | 40-45 | 49-52 | 29-31       | 27-33 | 17-19       | 25-27 | 51-56       | 31-35     | 31-40       | 13-15 |
|                       | Mean     | 58-67   | 50        | 39-25   | 48-5      | 43-37 | 50-33 | 30-33       | 29    | 18-25       | 26    | 54          | 33        | 35-5        | 14    |
| <i>H. matritense*</i> | N        | 25      | -         | 22      | 21        | -     | -     | -           | -     | -           | -     | 26          | 22        | -           | -     |
|                       | Range    | 61-6-75 | -         | 34-58-4 | (52-3)-69 | -     | -     | -           | -     | -           | -     | (52)-66-8   | (30)-45-1 | -           | -     |
|                       | Mean     | 68-97   | -         | 45-69   | 62-87     | -     | -     | -           | -     | -           | -     | 59-09       | 39-1      | -           | -     |
| <i>I. morgani</i>     | N=1      | 130     | 114       | 77      | 106       | 90    | 106   | 63          | 73    | 37          | 40    | 107         | 65        | 78          | 28    |
| <i>B. praecursor</i>  | Pak 1681 | -       | -         | (>36)   | 54        | 46    | -     | -           | -     | 16          | -     | (>46)       | (>28)     | -           | 14    |
|                       | Pak 788  | 63      | 55        | (>42)   | 52        | 46    | 54    | (>28)       | 33    | 19          | 29-5  | 57          | 34        | 38          | 15    |

TABLE 12. *Bugtirhinus praecursor*, calcaneum: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997).

| Calcaneum             |          |             |           |              |
|-----------------------|----------|-------------|-----------|--------------|
| Taxa                  |          | Tuber TD    | Tuber APD | min post APD |
| <i>A. beonensis</i>   | N        | 5           | 5         | 5            |
|                       | Range    | 44-48       | 68-77     | 50-60        |
|                       | Mean     | 45-6        | 73-8      | 56-4         |
| <i>Beg. grimmi</i>    | N=2      | 34-53       | 47 -      | 45-54        |
| <i>Bel. caucasica</i> | N=1      | 40          | 61        | 48-5         |
| <i>H. matritense*</i> | N        | 13          | 13        | -            |
|                       | Range    | (27-8)-41-6 | (50-5)-65 | -            |
|                       | Mean     | 36-85       | 59-08     | -            |
| <i>B. praecursor</i>  | Pak 1989 | 27          | 43        | 35           |

TABLE 13. *Bugtirhinus praecursor*, navicular: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997).

| Navicular             |          |         |           |       |       |         |                |
|-----------------------|----------|---------|-----------|-------|-------|---------|----------------|
| Taxa                  |          | TD      | APD       | H     |       |         | prox. art. APD |
|                       |          |         |           | ant.  | mid.  | post.   |                |
| <i>A. beonensis</i>   | N        | 6       | 6         | 7     | 7     | 6       | 6              |
|                       | Range    | 41-47   | 57-64     | 26-30 | 19-22 | 28-32   | 38-43          |
|                       | Mean     | 43-83   | 60-33     | 28    | 20-86 | 30-17   | 40-83          |
| <i>Beg. grimmi</i>    | N=1      | (47)    | (59)      | -     | 22    | 29      | 45             |
| <i>H. matritense*</i> | N        | 29      | 31        | -     | -     | 31      | -              |
|                       | Range    | 32-3-43 | 41-4-58-2 | -     | -     | 20-26-6 | -              |
|                       | Mean     | 37-77   | 50-44     | -     | -     | 24-28   | -              |
| <i>B. praecursor</i>  | Pak 1718 | 33      | 45        | 21    | 18    | 24      | 38             |

TABLE 14. *Bugtirhinus praecursor*, ectocuneiform: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997).

| Ectocuneiform          |                 |           |                 |           |           |                   |
|------------------------|-----------------|-----------|-----------------|-----------|-----------|-------------------|
| Taxa                   |                 | TD        | APD             | ant. H    |           | post. H           |
|                        |                 |           |                 | med.      | lat.      |                   |
| <i>A. beonensis</i>    | N               | 3         | 3               | 3         | 3         | 3                 |
|                        | Range           | 45-47     | 51-54           | 20-25     | 22-28     | 25-30             |
|                        | Mean            | 46        | 52.33           | 22.67     | 25        | 27.67             |
| <i>H. matritense</i> * | N               | 17        | 9               | -         | 15        | -                 |
|                        | Range           | 31.8-43.3 | 36-47.6         | -         | 17.5-25.7 | -                 |
|                        | Mean            | 39.92     | 42.75           | -         | 22.85     | -                 |
| <i>B. praecursor</i>   | <b>Pak 1992</b> | <b>30</b> | <b>(&gt;27)</b> | <b>14</b> | <b>14</b> | <b>(&gt;16.5)</b> |

cuneiforms row. The oval entocuneiform facet is partly detached from the rectangular mesocuneiform facet. Both facets are smoothly sagittally convex, and the former a little lift backwards. The ectocuneiform facet is triangular, with its antero-lateral part visible in anterior view.

The third cuneiform (Pak 1992) is small and rather high, forming a triangular prism (Table 14). Its surface lacks any tuberosity. The proximal side is totally articulated and corresponds to the navicular (Pl. 2, fig. 9). The anterior border is convex. The medial side bears three articular facets. The proximal one, in the posterior half of the bone, is crescentiform and corresponds to the mesocuneiform. The two distal facets, responding to the MtII, are aligned down to the distal border of the face. Between the three facets there is a shallow depression, clearly delimiting the facets. The lateral side is damaged, but nevertheless bears two cuboid facets. The antero-distal one is semi-circular, salient from the face. The postero-proximal one is too damaged to be described. The lower face, totally articulated, corresponds to the MtIII. Its outline forms a quadrant, with small postero-medial and large postero-lateral stripes lacking.

*Metatarsal bones.* These are still very small and slender. A distal half of a MtII is preserved (Pak 792), with a drop-shaped diaphysis section. Its lateral border is flat, with an antero-lateral vertical ridge. In anterior view, the trochlea axis is curved inwards. In distal view, the trochlea is narrow, deep, shorter medially than laterally (Table 15). Its lines are very blunt, rounded. The intermediate relief is very strong, high and acute in the posterior part, slightly visible in anterior view. The medial lip is very depressed, with a postero-medial expansion backwards. The trochlea is broader posteriorly, with a marked enlargement.

Three MtIII fragments have been found. The proximal end (Pak 1738) is smooth, slender, with narrow head and diaphysis (Table 16). In anterior view, the diaphysis narrows regularly from the epiphysis before becoming steady in the lower end of the preserved part (Pl. 2, fig. 10b). The upper border is concave, being much lower medially than laterally, and a slight inflection in the lateral border nearly gives a sigmoid outline to it (Pl. 2, fig. 10a). The upper side is exclusively articulated with the ectocuneiform and this facet bears exactly the same shape. Medially, two MtII facets are present, in contact with the proximal facet. Both are vertical and not fused. The postero-lateral side bears two MtIII facets, forming an angle of 135 degrees. The anterior one is vertical and triangular. On its top, a small triangular distinct facet responds to the cuboid in flexion movements and forms a smooth angle. The posterior facet is lower, oval and subvertical. The whole preserved part bears wide, keeled and flat contact zones with the MtII and MtIV on the diaphysis.

In both distal ends, the trochlea has a rounded anterior proximal border (Pl. 2, fig. 11), topped by a narrow and rather deep groove, and an asymmetrical end (lower medially). In distal view, the articular surface is nearly rectangular, slightly wider than deep (Table 16). The medial lip is still deeper than the lateral one. The intermediate relief is particularly strong and acute, visible in anterior view. It grows up to the posterior border of the trochlea. On both sides of the posterior top of the intermediate relief, there is a deep notch, hollowing the corresponding border of the trochlea.

The MtIV is represented by a right proximal end (Pak 1741), bearing traces of digestion. The bone is small and slender (Table 17), slightly curved outwards in the end of the preserved part (Pl. 2, fig. 12). The proximal end is wide, not so deep (APD), but the posterior part is damaged. In proximal view, the proximal side is quadrant-shaped, with a postero-medial centre. The medial side bears two facets, for the MtIII, forming an angle of 135 degrees. Starting from

TABLE 15. *Bugtirhinus praecursor*, MtII: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997).

| MtII                        |                |           |           |            |           |
|-----------------------------|----------------|-----------|-----------|------------|-----------|
| Taxa                        |                | diaphysis |           | dist. art. |           |
|                             |                | TD        | APD       | TD         | APD       |
| <i>A. beonensis</i>         | N              | 6         | 6         | 4          | 4         |
|                             | Range          | 23-28     | 20-26     | 33-37      | 32-36     |
|                             | Mean           | 26        | 23        | 34-75      | 34        |
| <i>Beg. grimmi</i>          | N=2            | 20-21     | 20-23     | -          | -         |
| <i>Bel. caucasica</i>       | N=1            | 20        | 19        | -          | -         |
| <i>H. matritense*</i>       | N              | 6         | 6         | 10         | 10        |
|                             | Range          | 19-5-22-5 | 18-21     | 25-6-28    | 25-5-30   |
|                             | Mean           | 20-87     | 19-37     | 26-65      | 28-11     |
| <b><i>B. praecursor</i></b> | <b>Pak 792</b> | <b>12</b> | <b>16</b> | <b>19</b>  | <b>21</b> |

TABLE 16. *Bugtirhinus praecursor*, MtIII: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997).

| MtIII                       |                 |             |             |           |           |           |            |           |
|-----------------------------|-----------------|-------------|-------------|-----------|-----------|-----------|------------|-----------|
| Taxa                        |                 | prox. art.  |             | diag. TD  | diaphysis |           | dist. art. |           |
|                             |                 | TD          | APD         |           | TD        | APD       | TD         | APD       |
| <i>A. beonensis</i>         | N               | 4           | 3           | 3         | 2         | 2         | 1          | 1         |
|                             | Range           | 48-52       | 42-44       | 31        | 37-38     | 22        | 45         | 37        |
|                             | Mean            | 50          | 43          | 31        | 37-5      | 22        | 45         | 37        |
| <i>Bel. caucasica</i>       | N=1             | 45          | 39          | 42        | 36        | 20        | 40         | 35        |
| <i>H. matritense*</i>       | N               | 23          | 11          | -         | 4         | 5         | 5          | 7         |
|                             | Range           | (32-5)-49-2 | (28)-43     | -         | 31-7-41   | 16-6-20   | (33)-45-8  | 30-8-37-1 |
|                             | Mean            | 43-08       | 36-18       | -         | 35-92     | 18-9      | 40-38      | 33-87     |
| <b><i>B. praecursor</i></b> | <b>Pak 1738</b> | <b>27-5</b> | <b>23-5</b> | <b>17</b> | <b>20</b> | <b>13</b> | <b>-</b>   | <b>-</b>  |
|                             | <b>Pak 2001</b> | <b>-</b>    | <b>-</b>    | <b>-</b>  | <b>-</b>  | <b>-</b>  | <b>25</b>  | <b>22</b> |
|                             | <b>Pak 2003</b> | <b>-</b>    | <b>-</b>    | <b>-</b>  | <b>-</b>  | <b>-</b>  | <b>26</b>  | <b>22</b> |

TABLE 17. *Bugtirhinus praecursor*, MtIV: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997).

| MtIV                        |                 |           |                 |               |                |          |            |          |          |           |           |
|-----------------------------|-----------------|-----------|-----------------|---------------|----------------|----------|------------|----------|----------|-----------|-----------|
| Taxa                        |                 | prox. end |                 | prox. art. TD | medial facets  |          |            |          |          | diaphysis |           |
|                             |                 | TD        | APD             |               | ant TD         | ant H    | post APD   | post H   | D        | TD        | APD       |
| <i>A. beonensis</i>         | N               | 4         | 4               | 4             | 3              | 2        | 4          | 4        | 4        | 4         | 4         |
|                             | Range           | 41-44     | 39-42           | 34-37         | 17-19          | 12-17    | 17-20      | 13-17    | 7-10     | 28        | 24-25     |
|                             | Mean            | 42-5      | 40-5            | 35-5          | 17-67          | 14-5     | 18         | 15       | 9        | 28        | 24-5      |
| <i>Beg. grimmi</i>          | N               | 4         | 4               | 5             | 5              | 5        | 4          | 4        | 4        | 2         | 2         |
|                             | Range           | 37-42     | 36-40           | 30-33         | 15-18          | 9-14     | 13-19      | 13-16    | 8-10     | 25        | 21-23     |
|                             | Mean            | 40        | 38-25           | 31-2          | 16-4           | 12-2     | 15-25      | 14-5     | 9        | 25        | 22        |
| <i>C. oettingenae</i>       | N=1             | 31        | 30              | 25            | 12             | 9        | 15         | 15       | 7        | -         | -         |
| <i>H. matritense*</i>       | N               | 11        | 10              | -             | -              | -        | -          | -        | -        | 7         | 7         |
|                             | Range           | 31-5-42   | 30-3-41-2       | -             | -              | -        | -          | -        | -        | 21-9-25-2 | 20-6-25   |
|                             | Mean            | 37-64     | 35-55           | -             | -              | -        | -          | -        | -        | 23-17     | 21-96     |
| <b><i>B. praecursor</i></b> | <b>Pak 1741</b> | <b>25</b> | <b>(&gt;20)</b> | <b>(20)</b>   | <b>(&gt;7)</b> | <b>7</b> | <b>(7)</b> | <b>6</b> | <b>5</b> | <b>17</b> | <b>14</b> |



TABLE 18. *Bugtirhinus praecursor*, second posterior medial phalanx: measurements and comparison with other Miocene elasmotheriines; \* after Iñigo and Cerdeño (1997).

| First posterior medial phalanges (MtlI) |          |           |           |           |           |             |             |
|---|----------|-----------|-----------|-----------|-----------|-------------|-------------|
| Taxa                                    |          | TD        |           | APD       |           | H           |             |
|   |          | prox.     | dist.     | prox.     | dist.     | max.        | min.        |
| <i>A. beonensis</i>                     | N=2      | 29-34     | 25-28     | 23-25     | 19-22     | 23-25       | 22-23       |
| <i>H. matritense</i> *                  | N        | 6         | 5         | 6         | 4         | 6           | -           |
|   | Range    | 27-9-29-5 | 23-25-1   | 24-4-26-6 | 19-3-20-2 | 25-4-30-2   | -           |
|   | Mean     | 28-63     | 24-38     | 25-59     | 19-77     | 28-3        | -           |
| <i>B. praecursor</i>                    | Pak 1746 | <b>22</b> | <b>20</b> | <b>15</b> | <b>14</b> | <b>15-5</b> | <b>14-5</b> |

the posterior facet and rather damaged, a continuous horizontal pad crosses the posterior side up to the developed postero-lateral tuberosity.

*Phalanx.* The second phalanx for the MtlI (Pak 1746) is small, deep and high, without tuberosities (Table 18).

#### SYSTEMATIC POSITION OF *BUGTIRHINUS PRAECURSOR*

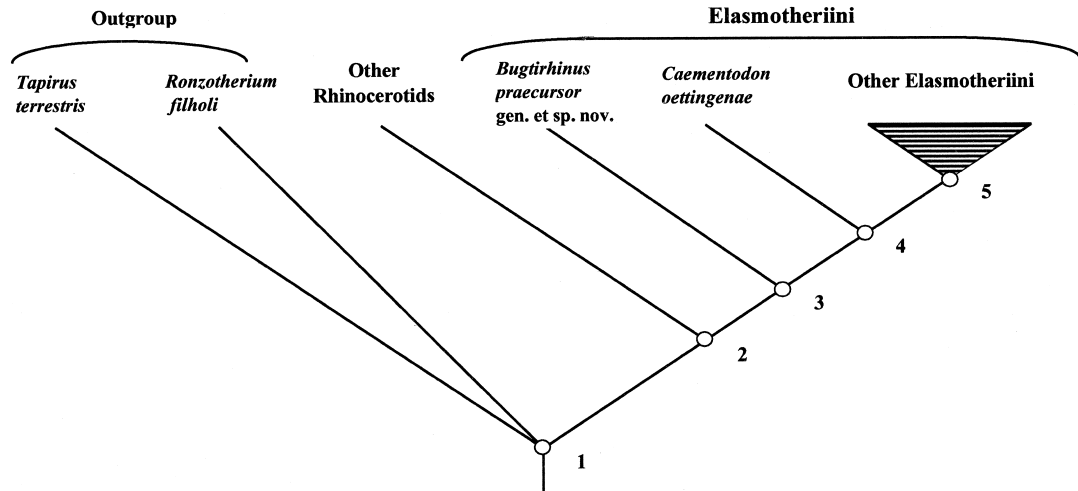
*Analysis.* The very small size (Tables 1–18) is characteristic of both teeth and postcranial skeleton of *B. praecursor*. It is smaller than other elasmotheriines and only comparable to the minute *Protaceratherium* from Eurasia (Roman 1924). The tiny *Caementodon oettingenae* is even larger (except for I1/, I2/, scaphoid, unciform and astragalus). Nevertheless, scaphoid and unciform reach the smallest dimensions observed for specimens of *Hispanotherium matritense* (juveniles).

Although there is an increase of the size from *B. praecursor* up to other elasmotheriines (Tables 1–18), there is no increase of robustness for carpus and tarsus (Tables 7–9, 11–14). The metapodials are more slender in *B. praecursor* than in the other elasmotheriines (Tables 10, 15–17). Moreover, their diaphyse and trochleae are deeper (greater APD) and comparable to the cursorial *Protaceratherium*, *Plesiaceratherium* and *Tapirus*. The high, narrow and deep phalanx (Table 18) shows the same trend, very distinct from *Aegyrcitherium beonensis*. On the unciform, the facet for the McV is very oblique transversally (Pl. 2, fig. 4). This functional orientation certainly corresponds to a reduced McV, as observed in *A. beonensis* (for which McV is known) and the extant rhinos. In it, they differ from those of the tetradactyl rhinocerotoids and tapiroids, where this facet is nearly horizontal. Contacts between the metapodials are long: *B. praecursor* was a tridactyl cursorial rhino, with a strong digitigrade tendency.

*Phylogeny.* Characters checked on teeth and postcranial bones of *B. praecursor* allow us to display cladistically the relationships of this new taxon (Text-fig. 4).

The cladogram shows that *B. praecursor* shares many synapomorphies (Text-fig. 4, node 3) with the other Elasmotheriini, but not with the primitive rhinocerotid *Ronzotherium filholi* and other rhinocerotids as a whole: semi-circular outlined I1/, cement filling up the cheek teeth, partially fused roots on upper cheek teeth, strong lingual wall on P2-4/, transverse metaloph on P2/, short metaloph on M1/ and especially M2, trefoil-shaped protoloph on M3/, absence of labial cingulum on lower cheek teeth, strong mesostyle on upper deciduous teeth, posterior contact between scaphoid and semilunate, oblique fibular facet on astragalus, high and narrow *Tuber calcanei*, rectangle-shaped navicular, sigmoid upper border on MtIII, and continuous pad-shaped posterior tuberosity on MtIV. These apomorphies mean that *B. praecursor* is truly an elasmotheriine.

Meanwhile, some apomorphic characters of the other Elasmotheriini are lacking: subhypodont cheek teeth, wide postfossette on upper premolars, absence of lingual cingulum on lower cheek teeth, articulated ulna and semilunate, which also characterize the '*Caementodon oettingenae*-other Elasmotheriini' clade



TEXT-FIG. 4. *Bugtirhinus praecursor* gen. et sp. nov.; phylogenetic relationships within the Elasmotheriini. Node 1, Outgroups. Node 2, Rhinocerotids. Node 3, semicircular outlined I1/, cement filling up the cheek teeth, partially fused roots on upper cheek teeth, strong lingual wall on P2-4/, transverse metaloph on P2/, short metaloph on M1/ and especially M2, trefoil-shaped protoloph on M3/, absence of labial cingulum on lower cheek teeth, strong mesostyle on upper deciduous teeth, posterior contact between scaphoid and semilunate, oblique fibular facet on astragalus, high and narrow *Tuber calcanei*, rectangle-shaped navicular, sigmoid upper border on MtIII, continuous pad-shaped posterior tuberosity on MtIV. Node 4, subhypsodont cheek teeth, wide postfossette on upper premolars, absence of lingual cingulum on lower cheek teeth, articulated ulna and semilunate. Node 5, secondary folds on cheek teeth, constriction on the ectometaloph of M3/, flat magnum facet on the scaphoid, deep incision between the medial facets of the magnum, high and narrow expansion on the Cc1 facet of the astragalus.

(Text-fig. 4, node 4), are absent in this species. Consequently, *B. praecursor* is the sister group of other Elasmotheriini. Moreover, no autapomorphy distinguishes the species. Hence, the diagnosis of the Elasmotheriini is that of *B. praecursor*.

The second dichotomy within Elasmotheriini (Text-fig. 4, node 5) sets *Caementodon oettingenae* Heissig, 1972 as the sister group of the remaining elasmotheriines. These latter taxa are defined by secondary folds on cheek teeth, constriction on the ectometaloph of M3/, flat magnum facet on the scaphoid, deep incision between the medial facets of the magnum, and high and narrow expansion on the Cc1 facet of the astragalus.

This paper states that *B. praecursor* and *C. oettingenae* are distinct from other Miocene elasmotheriines. Some authors (Heissig 1972, 1974, 1976, 1989; Chen 1977; Yan 1979; Guan 1988; Fortelius and Heissig 1989; Fortelius 1990; Antoine 1997; Welcomme *et al.* 1997) also consider *C. oettingenae* to be a distinct taxon. Others (Antunes and Ginsburg 1983; Cerdeño 1989, 1992, 1995, 1996; Prothero *et al.* 1989; Prothero and Schoch 1989; Cerdeño and Iñigo 1996; Iñigo and Cerdeño 1997) recognize only one valid elasmotherine genus in the lower and middle Miocene of Eurasia: *Hispanotherium* Crusafont and Villalta, 1947. Our results refute their hypothesis, at least for the genus *Caementodon* discussed in this paper (for further comments on the diversity of elasmotheriines, see Antoine, 1997).

Only dental and postcranial characters have been discussed so far, because cranial remains attributed to *B. praecursor* and *C. oettingenae* are entirely unknown. It is impossible to define the characteristics of the skull at the basal node of the Elasmotheriini.

*Origin and dispersion of the Elasmotheriini.* The phylogenetic interrelationships of the Elasmotheriini (Text-fig. 4) lead us to the following remarks.

*B. praecursor* is the most primitive elasmotheriine described so far. On the one hand, this species shares many exclusive characters with the other elasmotheriines. On the other hand, no autapomorphy

characterizes it. Thereby, for its known characters, *B. praecursor* constitutes the ancestral morphotype of the elasmotheriines. Moreover, we can deduce that the group itself is older. Localities with *B. praecursor* correspond to the lower part of the MN 3 (see above), but an uppermost Oligocene to a lowermost Miocene emergence is probable. Such localities are unknown in this area (the whole of the Miocene in the Dera Bugti syncline is younger than the Eurasia-Africa contact, at about 20 Ma) and very rare elsewhere. At the moment, the Bugti localities are the oldest known to contain elasmotheriines. Yet, Qiu (1990) pointed out the questionable presence of a primitive elasmotheriine in the earlier Aquitanian site of Xiejia (China). The referred material comprises a 'P4', a ?M/2, a P/2 and a MtIV, previously attributed to *Brachypotherium* sp. by Li and Qiu (1980). Our opinion is that these remains show no affinity with primitive elasmotheriines. Moreover, the metapodial belongs to a teleoceratine (*Aprotodon* sp.) more primitive than *Brachypotherium*. The upper tooth (*ibid.*, pl. 1, fig. 6) is a D4/ rather than a permanent premolar, which explains its small size. The P/2 and ?M/2 are not described or figured.

Because the most primitive elasmotheriines, *B. praecursor* and *C. oettingenae*, originate from Pakistan, an Indo-Pakistani differentiation for the group can be suggested. The first appearance of *C. oettingenae* was necessarily later than that of *B. praecursor*, and must have preceded that of other elasmotheriines. The earliest records outside the Bugti Hills are in Western Europe (Text-fig. 2): *H. matritense* is present in Córcoles (Spain) and *A. beonensis* in Pellecagus (France), at locations attributed to late MN 4a (Iñigo and Cerdeño 1997; Antoine *et al.* 2000). In Central Europe and Asia, the oldest sites are Belometchetskaya (Borissiak 1935, 1938; Gabunia 1981) and Tongxin (Guan 1988). Made (1996) correlated these localities with MN 5. Finally, *C. oettingenae* occurs all along the Chinji Formation (Pakistan), and is also present at Mochiwala (Lower Chinji) according to Heissig (1972). This locality corresponds to the upper part of the MN 5 (Made 1996). We can conclude that *C. oettingenae* was necessarily present during the MN 3 Zone. The Murree and Kamliyal formations (between the Dera Bugti Fm and the Chinji Fm), in Pakistan, should yield this elasmotheriine.

The first evidence of elasmotheriines in Western Europe are Pellecagus (Antoine *et al.* 2000) and Córcoles (Iñigo and Cerdeño 1997), in late early MN 4. Hence the dispersal of elasmotheriines towards Western Europe can be considered as subcontemporaneous with the arrival of *Prodeinotherium*, *Bunolistriodon*, *Dorcatherium* and *Megacricetodon*. All of these taxa have a previous record in Asia and/or Africa. This event corresponds to the second Proboscidean Datum Event (Tassy 1990), also called the 'Early Aragonian Faunal Exchange' by Made (1997).

*Acknowledgements.* The authors thank Prof. L. Ginsburg, F. Duranthon, M. Delcorso, M. Benammi and L. Marivaux for their participation in the French palaeontological expeditions of 1995–1999; Prof. P. Tassy (MNHN, Paris) for helpful corrections and discussion; and Nawab M. A. K. Bugti (Dera Bugti), H. E. I. Akhund (Karachi), Mr Delhavi (Pakistan Embassy, Paris), M. H. Shahwani, D. F. Baloch and A. R. Durrani (Quetta), Prof. Dr Kassi, Dr I. S. Baloch and D. M. Kakar (University of Baluchistan, Quetta), I. H. Haideri (GSP, Quetta), Dr P. Janvier (MNHN, Paris), Miss C. Sudre (Chief Curator, Muséum d'Histoire naturelle, Toulouse), F. Laudet (University of Montpellier), Prof. Dr V. Fahlbusch and Prof. Dr K. Heissig, Drs K. Peter, U. Göhlich and G. Rössner (BSP München), and Drs J. J. Hooker, A. Curren and P. J. Whybrow (NHM, London) for other help. They are grateful to Drs D. R. Prothero and M. Fortelius for their critical review and helpful comments.

## REFERENCES

- ANTOINE, P. O. 1997. *Aegycitherium beonensis* nov. gen. nov. sp., nouvel élasmothère (Mammalia, Rhinocerotidae) du gisement miocène (MN 4b) de Montréal-du-Gers (Gers, France). Position phylogénétique au sein des Elasmotheriini. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **204**, 399–414.
- BULOT, C. and GINSBURG, L. 2000. Une faune rare de rhinocérotidés (Mammalia, Perissodactyla) dans le Miocène inférieur de Pellecagus (Gers, France). *Geobios*, **33**, 249–255.
- ANTUNES, M. T. and GINSBURG, L. 1983. Les Rhinocérotidés du Miocène de Lisbonne. Systématique, écologie, paléobiogéographie, valeur stratigraphique. *Ciências da Terra*, **7**, 17–98.
- BELLAJEVA, E. I. 1971. On a rhinoceros (Rhinocerotidae), from the Neogene of Western Mongolia. *Fauna Mesozoya i Kainozoya Zapadnoy Mongolii*, **3**, 78–97. [In Russian].
- BONAPARTE, C. 1845. *Catalogo metodico dei mammiferi europei*. Giacomo Pirola, Milano, 36 pp.

- BORISSIAK, A. A. 1935. Neue materialien zur phylogenie der Dicerorhinae. *Comptes Rendus de l'Académie des Sciences de l'URSS*, **8**, 381–384.
- 1938. A new *Dicerorhinus* from the Middle Miocene of North Caucasus. *Travaux de l'Institut de Paléontologie de l'Académie des Sciences de l'URSS*, **8**, 7–62.
- BRUIJN, H. de, DAAMS, R., DAXNER-HÖCK, G., FAHLBUSCH, V., GINSBURG, L., MEIN, P. and MORALES, J. 1992. Report of the RCMNS working group on fossil mammals, Reisenburg 1990. *Newsletters on Stratigraphy*, **26**, 65–118.
- CERDEÑO, E. 1989. *Revision de la sistematica de los rinocerontes del Neogeno de Espana*. PhD thesis, Universidad Complutense (ed.), Madrid, 429 pp.
- 1992. Spanish Neogene rhinoceroses. *Palaeontology*, **35**, 297–308.
- 1995. Cladistic analysis of the family Rhinocerotidae (Perissodactyla). *American Museum Novitates*, **3143**, 1–25.
- 1996. Rhinocerotidae from the Middle Miocene of the Tung-gur Formation, Inner Mongolia (China). *American Museum Novitates*, **3184**, 1–43.
- and IÑIGO, C. 1996. *Hispanotherium matritense* (Rhinocerotidae) de la ciudad de Madrid (España) y su relación con el paleoambiente del Aragoniense medio (Mioceno medio). *Revista Española de Paleontología*, **12**, 80–90.
- CHEN GUANFANG 1977. A new genus of Iranotheriinae of Ningxia. *Vertebrata Palasiatica*, **15**, 143–147. [In Chinese].
- CRUSAFONT, M. and VILLALTA, J. F. 1947. Sobre un interesante rinoceronte (*Hispanotherium* nov. gen.) del Mioceno del valle de Manzanares. Nota preliminar. *Las Ciencias*, **12**, 869–883.
- CUVIER, G. 1822. *Recherches sur les ossements fossiles*. Edmond d'Ocagne (ed.), Paris, 435 pp.
- FISCHER, G. 1808. Sur *Elasmotherium*. *Programme Moscou*, **4**, 23.
- FLYNN, L. J., JACOBS, L. L. and CHEEMA, I. U. 1986. Baluchimyinae, a new ctenodactyloid rodent subfamily from the Miocene of Baluchistan. *American Museum Novitates*, **2841**, 1–25.
- FORSTER-COOPER, C. 1924. On the skull and dentition of *Paraceratherium bugtiense*: a genus of aberrant rhinoceros from the lower Miocene deposits of Dera Bugti. *Philosophical Transactions of the Royal Society of London, Series B*, **212**, 369–394.
- 1934. The extinct rhinoceroses of Baluchistan. *Philosophical Transactions of the Royal Society of London, Series B*, **223**, 569–616.
- FORTELIUS, M. 1990. Rhinocerotidae from Pasalar, middle Miocene of Anatolia (Turkey). *Journal of Human Evolution*, **19**, 489–508.
- and HEISSIG, K. 1989. The phylogenetic relationships of the Elasmotherini (Rhinocerotidae, Mamm.). *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie*, **29**, 227–233.
- GABUNIA, L. 1981. Traits essentiels de l'évolution des faunes de Mammifères néogènes de la région mer Noire-Caspienne. *Bulletin du Muséum National d'Histoire Naturelle, 4ème Série*, **3**, 195–204.
- GINSBURG, L., MAUBERT, F. and ANTUNES, M. T. 1987. Découverte d'*Hispanotherium* et de *Gaindatherium* (Rhinocerotidae, Mammalia) dans le Miocène de France. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, **9**, Section C, 303–311.
- GUAN JIAN 1988. The Miocene strata and mammals from Tongxin, Ningxia and Guanghe, Gansu. *Memoirs of the Beijing Natural History Museum*, **42**, 1–21.
- HEISSIG, K. 1969. Die Rhinocerotidae (Mammalia) aus der oberoligozänen Spaltenfüllung von Gaimersheim. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Neue Folge*, **138**, 1–133.
- 1972. Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. 5. Rhinocerotidae (Mamm.) aus den unteren und mittleren Siwalik-Schichten. *Abhandlungen der Bayerischen Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Klasse, Neue Folge*, **152**, 1–112.
- 1974. Neue Elasmotherini (Rhinocerotidae, Mammalia) aus dem Obermiozän Anatoliens. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie*, **14**, 21–35.
- 1976. Rhinocerotidae (Mammalia) aus der *Anchitherium*-Fauna Anatoliens. *Geologisches Jahrbuch, B*, **19**, 3–121.
- 1989. The Rhinocerotidae. 399–417. In PROTHERO, D. R. and SCHOCH, R. M. (eds). *The evolution of perissodactyls*. Oxford University Press, New York, 537 pp.
- HOOIJER, D. A. 1966. Miocene Rhinoceroses of East Africa. *Bulletin of the British Museum (Natural History). Geology Series*, **13**, 117–190.
- IÑIGO, C. and CERDEÑO, E. 1997. The *Hispanotherium matritense* (Rhinocerotidae) from Córcoles (Guadalajara, Spain): its contribution to the systematics of the Miocene Iranotheriina. *Geobios*, **30**, 243–266.
- JACOBS, L. L., CHEEMA, I. U. and SHAH, S. M. I. 1981. Zoogeographic implications of early Miocene rodents from the Bugti Beds, Baluchistan, Pakistan. *Geobios*, **15**, 101–103.
- LI CHUAN-KUEI and QIU ZHU-DING 1980. Early Miocene mammalian fossils of Xining Basin, Qinghai. *Vertebrata Palasiatica*, **18**, 210–218. [In Chinese, English abstract].

- LYDEKKER, R. 1881. Siwalik Rhinocerotidae. *Memoirs of the Geological Survey of India, Palaeontologica Indica, Series 10*, **2**, 1–62.
- 1884. Additional Siwalik Perissodactyla and Proboscidea. *Memoirs of the Geological Survey of India, Palaeontologica Indica, Series 10*, **3**, 1–34.
- MADDEN, C. T. and VAN COUVERING, J. A. 1976. The Proboscidean Datum Event: Early Miocene migration from Africa. *Geological Society of America, Abstracts with Programs*, 992.
- MADE, J. VAN DER 1996. Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. *Contributions to Tertiary and Quaternary Geology*, **33**, 3–254.
- 1997. Intercontinental dispersal events, eustatic sea level and Early and Middle Miocene stratigraphy. 75–82. In AGUILAR, J. P., LEGENDRE, S. and MICHAUX, J. (eds). Actes du Congrès BiochroM'97. *Mémoires et Travaux de l'Ecole Pratique des Hautes Etudes, Institut de Montpellier*, **21**, 1–806.
- MATTHEW, W. 1931. Critical observations on the phylogeny of the Rhinoceroses. *University of California Publications, Bulletin of the Department of Geological Sciences*, **20**, 1–9.
- MEIN, P. 1975. Résultat du groupe de travail des Vertébrés. 78–81. In SENES, J. (ed.). *Report on activity of the Regional Committee of the Mediterranean Neogene Stratigraphy Working Groups (1971–1975)*. Bratislava, 154 pp.
- 1979. Rapport d'activité du groupe de travail vertébrés; mise à jour de la biostratigraphie du Néogène basée sur les mammifères. *Annales Géologiques des Pays Helléniques, Hors-série*, 1367–1372.
- 1990. Updating of MN Zones. 73–90. In LINDSAY, E., FAHLBUSCH, V. and MEIN, P. (eds). *European Neogene mammal chronology*. Plenum Press, New York, 658 pp.
- OWEN, R. 1845. *Odontography*. Part 3. Hippolyte Baillière, 289–655.
- 1858. On the characters, principles of division, and primary groups of the class Mammalia. *Journal and Proceedings of the Linnean Society of London, Zoology*, **2**, 1–37.
- PICKFORD, M. 1986. Cainozoic palaeontological sites of western Kenya. *Münchner Geowissenschaftliche Abhandlungen A, Geologie und Paläontologie*, **8**, 1–151.
- 1988. The age(s) of Bugti fauna(s), Pakistan. 937–955. In UNIVERSITY OF HONG KONG (ed.). *The palaeoenvironment of East Asia from Mid-Tertiary*, **2**. University of Hong Kong.
- PILGRIM, G. E. 1908. The Tertiary and post-Tertiary freshwater deposits of Baluchistan and Sind, with notes of new vertebrates. Part 2. *India Geological Survey Records*, **37**, 39–166.
- 1910. Notice on new mammal genera and species from the Tertiaries of India. *Records of the Geological Survey of India*, **15**, 63–71.
- PILGRIM, G. E. 1912. The vertebrate fauna of the Gaj Series in the Bugti Hills and the Punjab. *Paleontologia Indica, New Series*, **4**, 1–83.
- PROTHERO, D. R., GUÉRIN, C. and MANNING, E. 1989. The history of the Rhinocerotidae. 322–340. In PROTHERO, D. R. and SCHOCH, R. M. (eds). *The evolution of perissodactyls*. Oxford University Press, New York, 537 pp.
- and SCHOCH, R. M. 1989. Classification of the perissodactyls. 530–537. In PROTHERO, D. R. and SCHOCH, R. M. (eds). *The evolution of perissodactyls*. Oxford University Press, New York, 537 pp.
- QIU, Z. 1990. The Chinese Neogene mammalian biochronology – its correlation with the European Neogene mammalian zonation. 527–556. In LINDSAY, E., FAHLBUSCH, V. and MEIN, P. (eds). *European Neogene mammal chronology*. Plenum Press, New York, 658 pp.
- RINGSTRÖM, T. J. 1923. *Sinotherium lagrelii*, a new fossil rhinocerotid from Shansi. *Bulletin of the Geological Survey of China, Series B*, **5**, 91–93.
- 1924. Nashörner der Hipparion-Fauna Nord-Chinas. *Geological Survey of China, Series C*, **11**, 1–156.
- RÖGL, F. 1996. Migration pathways between Africa and Eurasia – Oligocene–Miocene palaeogeography. *Europal*, **10**, 23–26.
- ROMAN, F. 1924. Contribution à l'étude de la faune de Mammifères des Littorinenkalk (Oligocène supérieur) du bassin de Mayence. Les Rhinocéros. *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon*, **7**, 1–54.
- SCHMIDT-KITTLER, N. 1987. The Carnivora (Fissipedia) from the lower Miocene of East Africa. *Palaeontographica A*, **197**, 85–126.
- TASSY, P. 1986. *Nouveaux Elephantoidea (Mammalia) dans le Miocène du Kenya*. Cahiers de Paléontologie, Editions du CNRS, Paris, 135 pp.
- 1990. The 'Proboscidean Datum Event': how many proboscideans and how many events? 237–252. In LINDSAY, E., FAHLBUSCH, V. and MEIN, P. (eds). *European mammal Neogene chronology*. NATO ASI Series, New York, 658 pp.
- WELCOMME, J. L., ANTOINE, P. O., DURANTHON, F., MEIN, P. and GINSBURG, L. 1997. Nouvelles découvertes de vertébrés miocènes dans le synclinal de Dera Bugti (Balouchistan, Pakistan). *Comptes Rendus de l'Académie des Sciences, Sciences de la Terre et des Planètes*, **325**, 531–536.

- and GINSBURG, L. 1997. Mise en évidence de l'Oligocène sur le territoire des Bugti (Balouchistan, Pakistan). *Comptes Rendus de l'Académie des Sciences, Sciences de la Terre et des Planètes*, **325**, 999–1004.
- MARIVAUX, L., ANTOINE, P. O. and BENAMMI, M. 1999. Mammifères fossiles des Collines Bugti. Nouvelles données. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **135**, 135–139.
- YAN DE-FA 1979. Einige der Fossilien Miozänen Säugetiere der Kreis von Fangxian in der Provinz Hupei. *Vertebrata PalAsiatica*, **17**, 189–199.

PIERRE-OLIVIER ANTOINE

JEAN-LOUP WELCOMME

Laboratoire de Paléontologie  
(UMR 8569 CNRS)

Muséum National d'Histoire naturelle  
8 rue Buffon  
F-75005 Paris Cedex, France

Typescript received 23 February 1999

Revised typescript received 7 February 2000